A NEW SPECIES OF *THYLACOLEO* (MARSUPIALIA: THYLACOLEONIDAE) WITH NOTES ON THE OCCURRENCES AND DISTRIBUTION OF THYLACOLEONIDAE IN SOUTH AUSTRALIA

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ABSTRACT

PLEDGE, NEVILLE S. 1975. A new species of *Thylacoleo* (Marsupialia: Thylacoleonidae), with notes on the occurrences and distribution of Thylacoleonidae in South Australia. *Rec. S. Aust. Mus.* 17 (16): 261-267.

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A new species, *Thylacoleo hilli*, is described from the Town Cave of Curramulka, South Australia, based on an upper carnassial P^3, which is about half the size of that of *T. carnifex* but otherwise almost identical. It is markedly larger than the Miocene species of *Wakaleo* Clemens & Plane, and because there is no indication of such a diminutive Pleistocene species, it is suggested that *T. hilli* is of Late Tertiary, possibly Miocene-Pliocene age.

A summary of the sites of thylacoleonid discoveries in South Australia is also presented.

INTRODUCTION

In 1956, the late Alan Hill collected an unusual tooth from the far recesses of the Town Cave (Y2) at Curramulka, on Yorke Peninsula, South Australia.

The Curramulka Town Cave had a natural 30 m shaft entrance which was enlarged so that the cave could be used as the town's water supply. The easier passages were explored early, bones being noted in passing. Germein (1960) published a popular account of his 1936 visit to the cave. In 1959, Messrs. B. Daily, G. Gross and P. Aitken of the South Australian Museum visited the cave, following reports from the Cave Exploration Group of South Australia (CEGSA) which examined it in 1956. Daily excavated lime- and sand-encrusted bone, including a partial skeleton of *Thylacoleo carnifex* (P12784) and a crushed skull of *Protemnodon* (P13027).

The cave is developed in the Early Cambrian Kulpara Limestone along a system of vertical joints that probably were originally open to the surface, such as those that can now be seen in the nearby council quarry. The fissures filled with sediment and debris, which became partly lithified as a tough, red bone-breccia. Subsequent ground water movement apparently re-excavated the fissures from the bottom, leaving high narrow passages roofed with breccia. Remains of Pleistocene marsupials have been found in this breccia and in the soft red silt that partially clogs some parts of the cave. It is from the latter that Daily's specimens were collected, in the section called the "Bedroom Chamber". Although it has not yet been properly prepared or identified, a cursory inspection of the fossil fauna suggests that it is of Late Pleistocene age. Hill's specimen, however, does not fit this hypothesis and suggests that at least some parts of the cave may date from Tertiary times. This is discussed below.

The tooth is interpreted to be the upper left carnassial (P^3) of *Thylacoleo*, but is so much smaller than that tooth in other members of the genus that it warrants the erection of a new species.

DESCRIPTION

Systematic Palaeontology:

Marsupialia
Phalangeroidea
Thylacoleonidae
Thylacoleo Owen
Thylacoleo hilli sp. nov.

Diagnosis: *Thylacoleo* with P^3 about half as long as in *T. carnifex*.

Holotype: upper left P^3, registered no. P18621 in the South Australian Museum.

Type locality: Town Cave (Y2), Curramulka, Yorke Peninsula.

Etymology: I have pleasure in naming this species for its finder, the late Alan Hill, a founding member of CEGSA in 1956, and a dynamic speleologist until his untimely death in 1972.

Description:

The only known specimen, P18621, an upper left P^3, measures 24·4 mm long which is less than half the length of the equivalent tooth of *Thylacoleo carnifex*. It has a long trenchant ridge, with the highest point over the anterior root (broken away). The height is 12·2 mm on the outer face. From here the crista descends abruptly on the anterior face to a point below the general base level of the crown, though not so obviously as in *T. carnifex*. Posteriorly from the anterior cusp, the crest descends gently (at about 20° below the horizontal, the base of the enamel being taken as horizontal) for a little more than halfway before abruptly levelling out to form the posterior "cusp" over the posterior root, then descends again at the same rate. In profile it is similar to P^3 of *T. carnifex*, although with less development of the anterior "cusp",

There are more obvious differences in occlusal view. In *Thylacoleo hilli*, P^3 is relatively broad and shows a rather tuberous outline in contrast to the more slender form of *T. carnifex*. However, the crest has the same sigmoid form, starting slightly mesiad at the anterior end and curving, convex outwards, to the anterior "cusp". Thence it is almost straight until the midway break-in-slope, where it bends slightly but sharply outwards to the posterior "cusp", after which it curves gently outwards to reach the posterior extremity. The sigmoid curve is thus rather more angular than in *T. carnifex*.

As in *Thylacoleo carnifex*, the anterior cusp is buttressed with a noticeable internal ridge and a somewhat more rounded external ridge, but in contrast to *T. carnifex*, this is not the widest part of the tooth. That point occurs

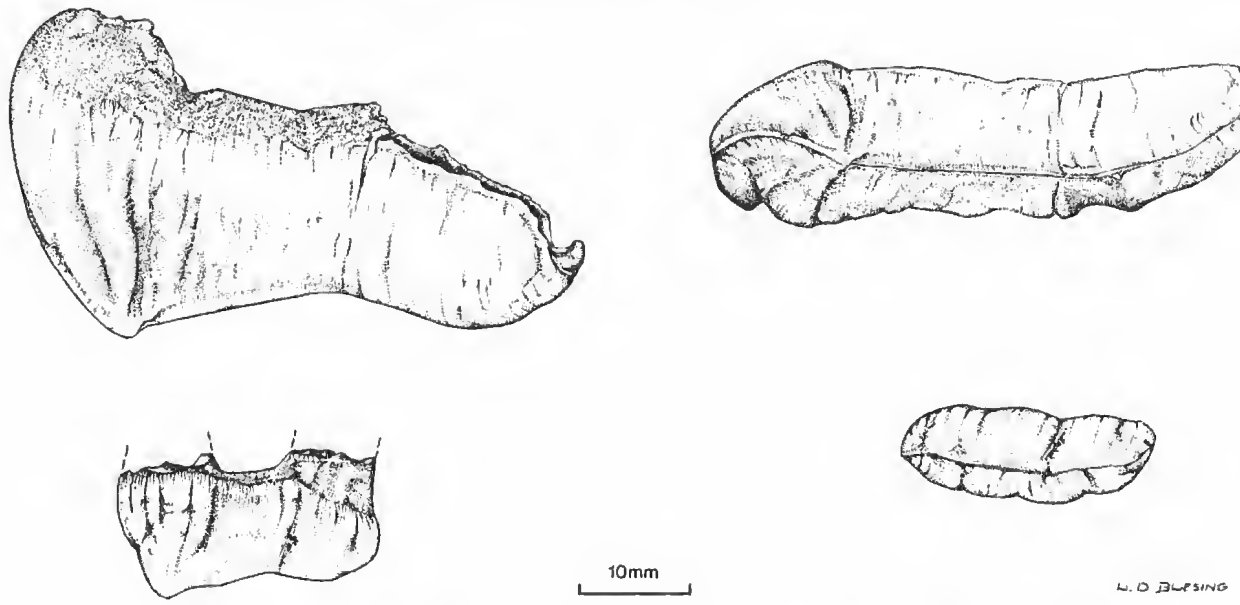
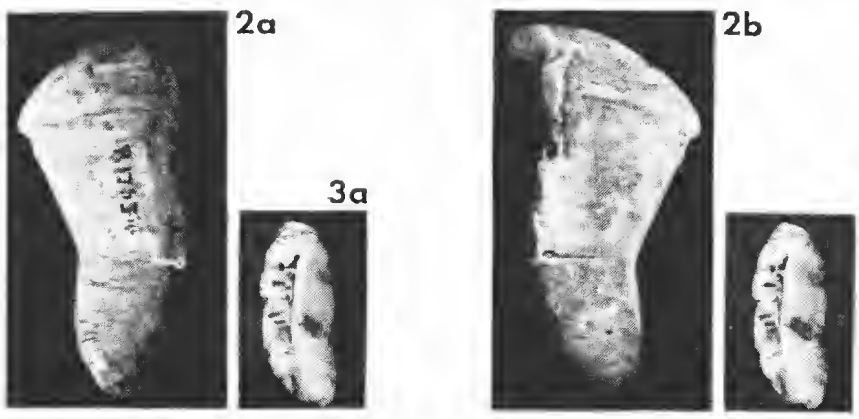


Fig. 1. Comparison of upper premolars of *Thylacoleo carnifex* P17654 (upper drawings) and *T. hilli* P18621, holotype, (lower drawings), in labial (left) and occlusal (right) views.



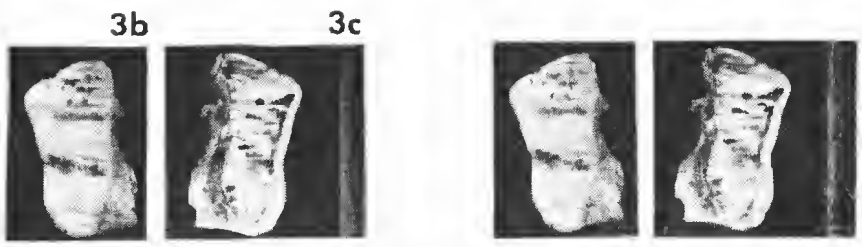


Fig. 2. *Thylacoleo carnifex* left P^3 (SAM P17654) a: labial view; b: lingual view. Natural size.

Fig. 3. *Thylacoleo hilli* n. sp. left P^3 (SAM P18621) Stereopairs; a: occlusal view; b: labial view; c: lingual view. Natural size.

slightly posterior to the cusp and just before the midpoint of the tooth. Again as in *T. carnifex*, the outer face is convex while the inner face is slightly hollow to maintain a constant sharp edge as tooth-wear progresses. This is particularly noticeable in the central region of the ridge, where tooth-wear has bevelled the inner face of the crest in a one-millimetre band. The hollow part of the face is apparently unworn, and is gently rugose in a vertical direction.

The anterior root appears to have been by far the stronger, although both are missing from the specimen. It has a deeply crescentic cross section at the base of the crown. There is no cingulum and the enamel thins and ends in a rather irregular line, as in *T. carnifex*.

Discussion: Apart from *Thylacoleo*, the only other form to which the Hill tooth could be compared is the lower premolar (P_3) of *Protemnodon* spp. (see Bartholomai 1974), but the differences in size and form (*Protemnodon* is too small, too flat-bladed and too narrow, and lacks the anterior descension of the crown enamel) are too obvious for this to seriously considered.

The possibility has been considered that the Town Cave tooth is an abnormal development. Various abnormalities of marsupial teeth have been discussed by Archer (1975) but the only type of interest here is the ephemeral tooth: that which may be present in embryo, but normally is resorbed or shed in young juveniles. There does not seem to be any certain way of distinguishing an isolated, unusually small tooth as a deciduous or ephemeral tooth. In the present instance, however, it is likely that this possibility can be discounted, for several reasons: (1) the tooth is well calcified and had well-developed roots (by contrast, some specimens of unworn *T. carnifex* premolars have very thin walled, fragile roots), (2) the enamel is thick and solid, (3) the tooth was functional, having a small but well-defined wear facet.

The Thylacoleonidae have a relatively long history, which unfortunately is poorly represented for most of its length. A single undescribed toothless palate from the Miocene Etadunna Formation (Ngapakaldi local fauna) (Stirton, Tedford and Woodburne 1968) in the Lake Eyre Basin, seems to be the first possible representative (Clemens and Plane 1974:659). This is followed by the two species of *Wakaleo* (Clemens and Plane 1974) from later Miocene deposits; then by the rather poorly known *Thylacoleo crassidentatus* (Bartholomai 1962) from the Pliocene Chinchilla Formation of the Western Darling Downs in Queensland. There is also an unidentified specimen from the Lower Pliocene Allingham Formation of north Queensland (Archer & Wade 1976:390), in which P^3 is relatively shorter than in *T. crassidentatus*, but larger than that estimated for *T. hilli* (M. Archer, pers. comm., 11.ii.75). The Allingham species has been compared with a specimen from Balladonia, W.A., mentioned by Merrilees (1968:14). The best known species, *Thylacoleo carnifex* (Owen 1859), is widespread in Australian Pleistocene cave deposits and in some other open situations (see Gill 1954).

Thylacoleo was an unusual animal in many ways, one of which was the apparent lack of deciduous cheek-teeth. Most notably, the large sectorial premolars apparently had no functional precursors, and persisted from the pouch stage to senility (Finch 1971). In two specimens in the South Australian Museum (P13721, P13829), these full-sized carnassials are almost fully erupted in jaws that are only 22-23 mm deep at the posterior end of the P_3 alveolus, and 85-90 mm long from the incisor alveolus to the angular process. Mandibles of mature *T. carnifex* reach a depth, at the P_3 alveolar margin, of up to 53 mm. The premolars are, therefore, apparently functional even in pouch young, although the two specimens mentioned above show no signs of wear. It is thus unlikely that the Curramulka tooth, *T. hilli*, which is slightly worn and has well-developed roots, is deciduous.

It is impossible, however, to present conclusive evidence one way or the other as to whether the tooth in question is permanent or deciduous. On the one hand, there is a slight indication that it could be deciduous by comparison with its postulated closest relatives. Woods (1956:138) has indicated its phalangeroid affinities, and certainly the jaw of *Wakaleo oldfieldi* bears some similarities in form with, say *Burramys*, which Broom (1898) concluded was close to the ancestral condition of the Thylacoleonidae. Many groups of phalangeroids have diminutive deciduous premolars (e.g. SAM M5539, a juvenile *Trichosurus vulpecula* with dP3, M1-3, and P3 unerupted below dP3.). At the same time, a koala M4625 has only the premolar and M1 fully erupted, and these premolars are identical in size and form with those in adult, even senile, individuals which suggests that the deciduous premolar, if it existed, was of very short duration. A deciduous cheek tooth in a koala embryo was noted by an early German embryologist (M. Archer, pers. comm., Nov. 1976).

On the other hand, there is good circumstantial evidence against the Hill tooth being deciduous, in that for all the scores of specimens

TABLE 1

Lengths of premolars of Thylacoleonidae (calculated parameters are based on the ratio for *T. carnifex* $P^3:P_3 = 1.295$)

Species	Carnassial Length			
	P^3		P_3	
	Range	Mean	Range	Mean
Thylacoleo carnifex—				
Darling Downs (Woods, 1956)	35·3-40·7	38·6 (N = 4)	49·8-53·8	51·7 (N = 3)
Wellington Caves (Australian Museum coll.)	35·7-46·0	39·8 (N = 48)	47·0-54·1	50·7 (N = 23)
Naracoorte Caves (S. Aust. Mus. coll.)	37·1-41·6	39·6 (N = 24)	49·2-54·5	52·2 (N = 14)
Total sample	35·3-46·0	39·6 (N = 76)	47·0-54·5	51·3 (N = 40)
T. crassidentatus—(Bartholomai, 1962)	35·6-41·4	37·5 (N = 4)		calc. 48·6
T. hilli n. sp.		calc. 18·8		24·4
Wakaleo vanderleuri (range of estimates)		13·5-15·3 (N = 1)		calc. 17·5-19·8
W. oldfieldi		12·4		calc. 16·1

of *Thylacoleo carnifex*, at all stages of development, there is no other tooth of similar size known. Also, the roots were not being resorbed. Accordingly, the easiest explanation is that it is a valid diminutive species.

Thylacoleo hilli gives the impression of being more akin to *Thylacoleo carnifex*. While there is an obvious similarity shown between the mandibles of *Wakaleo* and *Thylacoleo carnifex*, the P_3 of the former is of different proportions, being relatively shorter, while the molars are relatively larger and better developed (Clemens and Plane 1974). In contrast, the P^3 of *Thylacoleo hilli* is proportionally and morphologically closely similar to *T. carnifex* (see Fig. 1). It is not yet possible to compare directly the premolars of *Wakaleo* and *T. hilli*, but estimates of the size of the unknown premolars can be made, assuming that a regular size relationship between the upper and lower premolars of *T. carnifex* persists throughout the family. A large sample of premolars of *T. carnifex* in the Australian Museum, mostly from the Wellington Caves, and a somewhat smaller collection from the Naracoorte Caves, held by the South Australian Museum, have been measured, and using also the data in Woods (1956), the mean lengths of the upper and lowers calculated. The assumption was then made that the ratio of these two measurements ($P^3:P_3$) has been more or less constant at about 1.3. Using this constant, the lengths of P_3 of *Thylacoleo hilli* and P^3 of *Wakaleo* spp. have been calculated (see Table 1). It is seen that the premolar of *T. hilli* is closer in size to *Wakaleo* than to *T. carnifex*. However, as discussed above, its form is nearer to the latter. It is therefore more probably an ancestor of *T. carnifex*, and closer in time to *Wakaleo* than *T. carnifex*, but unlikely to be a descendant of *Wakaleo*. Clemens and Plane (1974) consider *Wakaleo* probably was not directly ancestral to *Thylacoleo carnifex*, and that thylacoleonid phylogeny was a plexus of lineages rather than a single line. *Thylacoleo hilli* would then represent a short twig near the axis of this plexus.

Age: The age of *T. hilli* is unknown, though presumably late Tertiary. It is unlikely to be Pleistocene, as there is no indication of it in any of the rich Pleistocene faunas known from Australia. It is not the same as the Balladonia *Thylacoleo* (Merrilees 1968; Archer & Wade 1976) which is regarded as Pleistocene. Nor is it likely to be a dwarfed Pleistocene species, produced by insular isolation in the same way as the pigmy elephants of some Mediterranean islands (e.g. Kurtén 1968:135), for although Curramulka is in the middle of the low and elongate Yorke Peninsula, there is no evidence that this has been an island at any time during the Cainozoic, and certainly not during the Pleistocene. Furthermore *T. carnifex* has been found in contiguous areas, such as Port Pirie and the Flinders Ranges, as well as in the Curramulka Town Cave itself and elsewhere on Yorke Peninsula. By comparison with the phylogenetic pattern of the Diprotodontidae (Stirton *et. al.* 1967) with its Pleistocene gigantism, and its absence from the late Pliocene Chinchilla and Mampuwordu sands, I suggest that *T. hilli* lived in late Miocene or early Pliocene times. However, this cannot be confirmed until more material and other associated species of the same age are found. Attempts to find the actual site within the cave, to collect more material, have so far been unsuccessful.

THYLACOLEONIDAE IN SOUTH AUSTRALIA

The discoveries of thylacoleonid fossils in South Australia are summarised in Table 2, and their distribution is shown in Fig. 4.

Remains of *Thylacoleo carnifex* were first reported from South Australia by Waterhouse (1879) in his annual report to the South Australian Institute. These were found, with *Diprotodon* "*Phascolomys*" (*Phascolonus gigas*) and *Macropus* by Mr. R. M. Robertson in a spring bog deposit in Salt Creek near Normanville. This deposit continued to yield bones until Zietz (1907) apparently worked it out with the discovery of more *Thylacoleo*. Zietz (1889) had previously reported *Thylacoleo* with *Diprotodon* from dam excavations at "Yam Creek, Bundaree". Gill (1954), unable to locate this place on a map, considered it a misspelling of Bungaree, but study of Museum reports shows that the site was at Bundey, about 40 km west of Morgan.

In the early 1900's, a fragment of *Thylacoleo carnifex* was found with other bones on the gravel bars of the Warburton River, near (old) Kalamurina. The source of these bones is probably the eroding channel deposits known as the Katipiri Sands (Stirton, Tedford & Miller 1961). This formation has yielded a single tooth at Lake Kanunka (idem) south of the Warburton River. Other open sites yielding *Thylacoleo* have been found in recent years: near Port Pirie, and at Lake Fowler, Yorke Peninsula.

At the turn of the century, *Thylacoleo* was found in cave deposits when William Reddan, Curator of the Naracoorte Caves, started excavating there, particularly in Alexandra Cave.

Zietz later undertook excavations in "Specimen Cave" and found considerable quantities of material. In recent years, better specimens have been collected from several other caves in the Naracoorte area: Haystall Cave (Pledge *et al.* unpubl.), Henschke's Quarry cave (Pledge in prep.), and particularly Victoria Cave (Smith 1971:185).

TABLE 2

Summary of distribution and discoveries of Thylacoleonidae in South Australia.

Locality	Type of Deposit	Collector	Year	Reference
Thylacoleo carnifex—				
Salt Creek, Normanville	Spring swamp	R. M. Robertson	1878	Waterhouse (1879)
Salt Creek, Normanville	Spring swamp	A. H. R. Zietz	1907	Zietz (1907)
Bundey, west of Morgan	Fluviatile (loam)	?	1889	Zietz (1890)
Kalamurina, Warburton R.	Fluviatile (channel?)	E. A. King	1905	S.A. Museum Report (1905-1906)
Alexandra Cave (U3), Naracoorte	Cave earth	Wm. Reddan	1900, 1907, 1912	
Specimen Cave (U35), Naracoorte	Cave earth	F. R. Zietz	1916	
Moorak, Mount Gambier	?(Well)	Campbell	1913	
Derrington Street, Mount Gambier	Cave	D. W. P. Corbett	1963	
James Quarry (U29), Naracoorte	Cave	N. B. Tindale and P. F. Lawson	1956	Daily (1961)
James Quarry (U29), Naracoorte	Cave	B. Daily, P. Aitken	1959	
Cathedral Cave (U12/13), Naracoorte	Cave earth	B. Daily	1959	
Town Cave (Y2), Curramulka	Cave earth	R. Sexton	1958	
Town Cave (Y2), Curramulka	Cave earth	B. Daily	1959	
Haystall Cave (U23), Naracoorte	Cave earth	N. Pledge *et al.*	1964	
Quarry, Curramulka	Fissure bone breccia	G. Pretty and N. Pledge	1967	
Fox Cave (U22), Naracoorte	Cave earth	F. W. Aslin	1968	
Mairs Cave (F3), Buckalowie Creek	Cave travertine	B. Daily *et al.*	1968	
Henschke's Quarry cave, Naracoorte (U91/97)	Cave earth	N. Pledge and F. Aslin	1969	
Victoria Cave (U1), Naracoorte	Cave earth	R. T. Wells *et al.*	1969	Smith (1971)
Port Pirie	Fluviatile (channel)	R. Elding	1973	
Lake Fowler, Yorke Peninsula	Gypsum lunette	J. McNamara	1975	
Thylacoleo hilli—				
Town Cave (Y2), Curramulka	Cave earth	A. Hill	1956	This paper
Wakaleo oldfieldi—				
Leaf locality, UCMP V6213, Lake Ngapakaldi	Wipajiri Formation, fluviatile (channel)	W. A. Clemens *et al.*	1971	Clemens and Plane (1974)

(Symbols such as U3, Y2, etc. are the official code numbers of caves as listed in the caves register of the Cave Exploration Group of South Australia, Inc.)

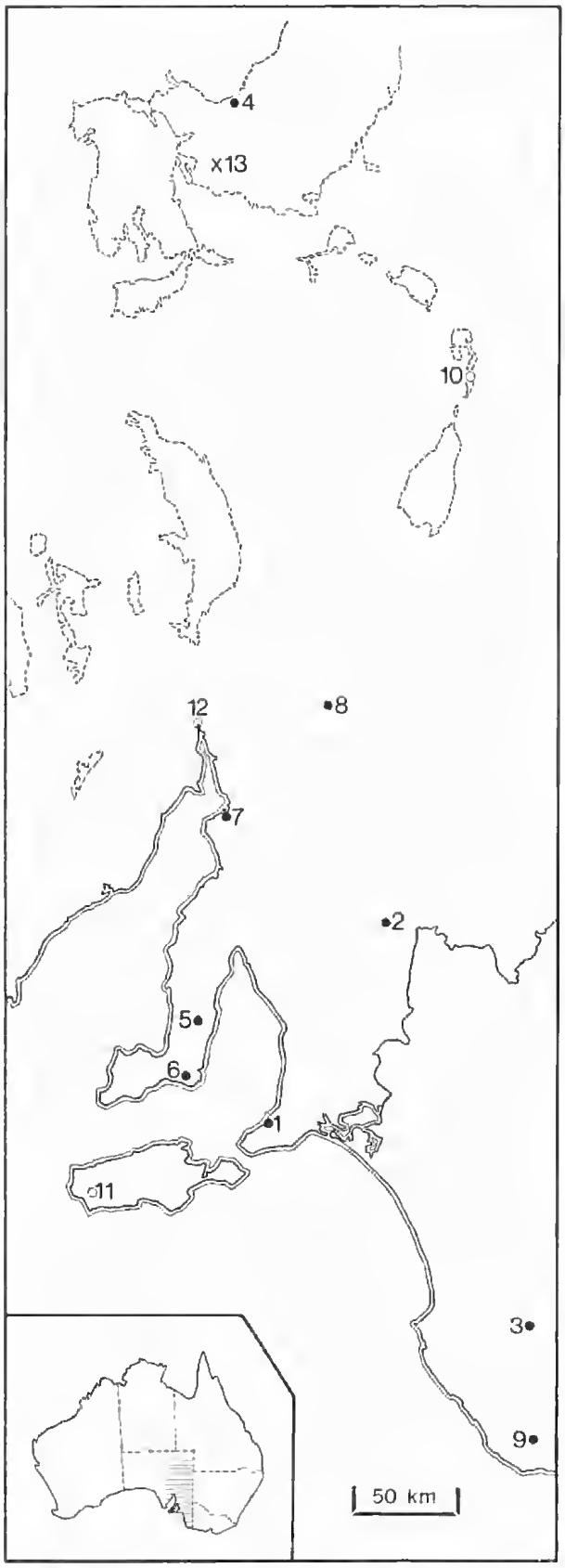


Fig. 4. Occurrences of Thylacoleonidae specimens in South Australia. ●: *Thylacoleo carnifex* ○: no record for the site, ×: *Wakaleo oldfieldi*. 1. Normanville, 2. Bundey, 3. Naracoorte, 4. Kalamurina (Warburton River), 5. Curramulka, 6. Lake Fowler, 7. Port Pirie, 8. Buckalowie Caves, 9. Mt. Gambier, 10. Lake Callabonna, 11. Rocky River, 12. Port Augusta, 13. Lake Ngapakaldi.

Partial skeletons were recovered from Cathedral Cave and from the two small caves in James Quarry, Naracoorte (Daily, 1960). The quarry and Town Cave at Curramulka on Yorke Peninsula, and Mairs Cave on Buckalowie Creek in the Flinders Ranges have also yielded some good material of *Thylacoleo carnifex*. *Wakaleo oldfieldi* was found in the Miocene Wipajiri Formation channel deposits at Lake Ngapakaldi (Clemens & Plane 1974).

Possibly more interesting than the occurrences outlined above are those richly fossiliferous areas where *Thylacoleo carnifex* has not been found. The species is apparently rare in the channel deposits intersected by the Warburton River and Cooper Creek. It is absent from the rich (though as yet poorly investigated) swamp deposits at Rocky River, Kangaroo Island, (Tindale, Fenner & Hall 1935) and has not been found in any of the cave deposits nearby. Most notably, there has been no sign of it (or any other carnivore) in the vast *Diprotodon* "graveyard" of Lake Callabonna. At the Salt Creek (Normanville) site, broken bones bearing distinct tooth or cut marks were recovered: these have been ascribed to *Thylacoleo* by A. Zietz (unpubl. note, 1907). No such indications have been reported from the Callabona fossils. No explanation has been offered for these apparent gaps in the range of *Thylacoleo carnifex*, and none will be attempted here, save that the reason may have some bearing on the animals way of life, which is still speculative.

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